# QUANTITATIVE DETERMINATION OF RHYTHMICITY IN ORGANISMS

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Within recent years increasing attention has been paid to the analysis of periodic activity of animals under controlled conditions by ecologists, and to periodic rhythms within the organism by physiologists. This general subject has been recently discussed (1), but there are several aspects of general organismal activity which need additional emphasis.

It is quite clear that there are several categories of activity; second, that this activity pattern of a species is complex and specific; third, that the activity pattern can be modified by the environment. The last two generalizations are obvious, but the first should be examined. Periodic environments are in general inhabited by species having periodic activity patterns, while certain social species and those species living in relatively constant environments tend to have an arhythmic activity pattern. The various permutations of organismal activity may be arranged within the following outline of diel patterns:

I. RHYTHMIC ACTIVITY (Periodic Activity).
   An activity pattern in which the fundamental characteristics of the activity-inactivity curve for a species population recur through successive day-nights (diel periods).
   1. *Environmental Type* (Exogenous Type).
      Periodic activity in which the pattern is directly induced by, and controlled by, the periodic environmental factors.
   2. *Endogenous Type.*
      Periodic activity in which the pattern is resident in the protoplasm, therefore more deeply-seated, and not directly induced by, but may be modified by, the environment.
      a. *Habitual Activity.*
         Endogenous activity which is the result of past experience, or induction in the individual, and consequently indirectly induced by the environment.
      b. *Inherent Activity* (Instinctive Activity ?).
         Endogenous activity which is a part of the species heredity.
   3. *Composite Type.*
      Periodic activity in which the pattern is in part exogenous, and in part endogenous.

II. Arhythmic Activity (Aperiodic Activity).

Activity of a species population, the individuals of which do not exhibit an average periodic pattern, but in which each individual exhibits a varying activity through successive day-nights.

The experimental findings for these several categories have been sorted in the discussion alluded to. Obviously such an outline is an expedient scheme, as well as a logical one. It is designed for laboratory analysis, since the proper placing of a pattern cannot be definitely made on uncontrolled data. For example, the overwhelming majority of animals has a periodic activity, but whether a particular individual has its pattern induced and controlled by the environment, or has an endogenous pattern, can be discovered only by placing the animal in a constant environment. Under constant conditions, if the pattern persists the activity may be habitual or inherent, and these two types can be separated with certainty only by breeding the species under constant conditions. It is also obvious that objective recording apparatus must be employed, preferably electrical apparatus, utilizing either a continuous record, or if a drum is used then its diameter and speed adjusted so that activity peaks will not obscure each other. Complete control is desirable, as well as non-disturbance of the animal through the changing of records, replenishing food and water supplies, noise, *et cetera*. The possibility of indirect tutelage and learning or induction of various kinds, as well as the operation of little known physical influences should be realized, and where possible guarded against. I am inclined to suggest that nothing more than a bare start has been made in the method of attack on the problem, or in the accumulation of critical information.

To implement the assignment of activity pattern, the following mathematical suggestion is made:

Let: A. *Amplitude* of a twenty-four hour (diel) cycle.
F. *Frequency* of a twenty-four hour (diel) cycle.
A. I. *Activity Index.*
T. A given twenty-four hour trial.
K. Trials run under constant environmental conditions.
R. Trials run under the normal fluctuating environmental conditions.
a. *Actant.* An actant is the percentage for any given hour of the total activity for that diel cycle, the total activity for the cycle equaling 100%.

d. *Diant.* A diurnal actant.
n. *Noctant.* A nocturnal actant.
v. *Vocant.* An actant which is measured by vocalization, stridulation or other sound production, rather than by movements of the animal.
p. *Populant.* The average actant of a population.
N. Average of the noctant gain over 50% activity for a diel cycle.
D. Average of the diant gain over 50% activity for a diel cycle.
$0^n$ Number of trials out of a given experiment (ten trials suggested) which show a nocturnal gain.
$0^d$ Number of trials out of a given experiment (ten trials suggested) which show a diurnal gain.

The following figure (Fig. 1) gives graphical expression to some of these terms which have been suggested to (1) facilitate

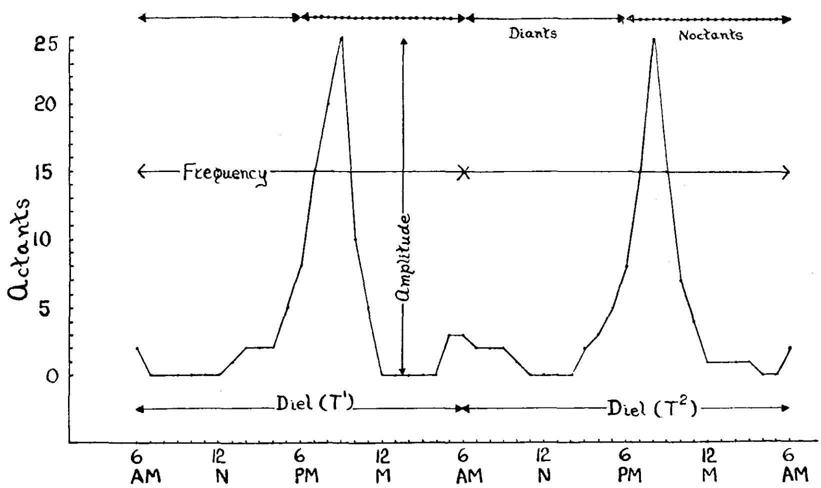


Fig. 1. Structure of a Typical Activity-inactivity Curve, Over Two Diel Periods, for a Hypothetical Nocturnal Animal.

the formulation of a mathematical approach to the study of diel periodicity, and (2) bring order to a rapidly expanding research field. A tentative formulation follows:

$$\frac{N\,0^n}{D\,0^d} = \text{A. I.}\left(\text{at } T^{10\ (\text{R or K})}\right)$$

I. Where individual activity is being measured by recorders in the field, or under normal fluctuating environmental factors, the application of this formula to the activity units collected will serve to separate those animals having a periodic activity from those having arhythmic activity. Where population activity is being studied special criteria will be employed which, when stated as populants, can be directly compared with recorded activity.

II. Where activity is being studied in the laboratory under "constant" conditions, the same formula will serve to (1) separate arhythmic from endogenous activity, where the latter is synchronized with the diel cycle, e. g., on a twenty-four hour frequency; (2) estimate quantitatively the degree of nocturnal or diurnal endogenosity of such synchronized activity; (3) measure loss of amplitude in successive diels if the actants are analyzed in successive samples where synchronized periodic activity is involved.

III. To separate habitual from inherent endogenosity, the animals must be bred in the constant experimental conditions, shielding the new generation from contact or tutelage of parent or parents, and application of the formula. Under these conditions, periodic activity in the generation thus born will be inherent activity in the strict sense. This is difficult to accomplish but oviparous invertebrates would appear to be the best research material for such an attack.

This formula will not anlayze unsynchronized activity rhythms, e. g., 25 hour periodism, *et cetera*, since in such a species, the cycle would shift through time on successive diels. Under such conditions, the first sample might show an endogenous diurnality, but a larger sample, involving fifty trials, might show an arhythmic activity index although the rhythm would be intact. This would be a consequence of the shift in noctant-diant ratio.

In addition to rhythms not on a twenty-four hour frequency, there is also the possibility of rhythm with a varying frequency. In both such possibilities a much more complex formulation will have to be applied.

For activity patterns synchronized on the diel rhythm, the simple formula will analyze the activity curve on a quantitative basis in terms of actants but to employ the formula, night and day must be definitely limited since the length of day and night varies regularly with latitude and time of year. There are numerous ways in which day and night can be arbitrarily fixed, depending upon the type of investigation being pursued. For example, nocturnal activity may be said to be the activity (1) between sunset and sunrise, either on an astronomical basis or on an arbitrary photometric standard of so many foot-candles, at a given latitude and time of year, in which case this designation of nocturnal may have to be factored, or (2) average sunset to average sunrise at a specific latitude and time of year, or (3) for experimental purposes some arbitrary designation, as from 6:00 P. M. to 6:00 A. M., *et cetera*. Similarly diurnal activity would then be the converse of any one form of designation adopted for nocturnal activity.

In the second place, ten complete diel periods are given in the above formula, merely as a suggestion. Ten trials may be sufficient, or a thousand trials may be necessary. Experience in frequent sampling of the data will demonstrate how many trials are needed to give an accurate activity index of a species activity pattern.

The terms N and D of the formula must be understood. If ten diels are used, the actants for each diel are determined and then, using the standard day and night decided upon, the actants are separated into diants and noctants respectively. Obviously, in an arhythmic species the diants and noctants tend to equal each other, in a nocturnal species the noctants are many and diants few, in a diurnal species the diants are many and the noctants few. N, the average gain in nocturnality, is the average of the noctants of the ten trials over 50% activity. Thus a species with a theroetical 100% nocturnality, would have a net average of 50%, while an animal with 80% nocturnality, would have a net average of 20%, etc. D is formed in the same way as N, using the diants instead of noctants.

It is necessary to express our activity data in some such way as per cent. This is due to increasing investigation on different kinds of animals, using many different kinds of recorders. Thus data are available in the form of vocalization-rate, distance moved per time unit, number of movements per time unit, various activity units, and so on, so that only a percentage figure, like the actant or its variants, is suitable for direct comparison. To further clarify the method, several hypothetical examples are given:

EXAMPLE 1. Animal exhibiting 100% nocturnal endogenosity.
10 diels with 50% noctant gain each (maximum):

$$\frac{50 \times 10}{0 \times 0} = \text{A.I. } \infty$$

Mathematically, this is the upper limit of the activity index, and to my knowledge has not yet been demonstrated for any species, although many species have a high A. I.

EXAMPLE 2. Animal exhibiting no periodicity, e. g. arhythmic. 10 diels with 5 of them having a 50% noctant gain, and 5 of them having a 50% diant gain, or some similar combination in which no net gain could be demonstrated for the experiment.

$$\frac{5 \times 50}{5 \times 50} = \text{A. I. of 1.}$$

Where the A. I. approaches unity, arhythmicity is demonstrated. All arhythmic species under constant conditions show such a low activity index.

EXAMPLE 3. Animal exhibiting 100% diurnal endogenosity. 10 diels with 50% diant gain each (maximum) :

$$\frac{0 \times 0}{50 \times 10} = \text{A. I. of 0}$$

Mathematically, this is the lower limit of the activity index, the latter having a spread from $\infty$ to 0, with perfect arhythmicity at the median point.

Once the absence of periodicity, or its presence is known, then by shift from constant conditions to conditions involving one varying influence at a time, the degree of exogenosity and endogenosity may be determined, etc.

The following table (Table I) gives several A. I. which have been determined experimentally within recent years:

TABLE I

EXAMPLE OF ACTIVITY INDEX

| ANIMAL | CATEGORY OF ADULT | A. I. | CALCULATED FROM |
|---|---|---|---|
| *Cambarus pellucidus* | Arhythmic | 3.4 | (2) |
| *Tamais striatus griseus* | Endogenous diurnal | 0.0102 | (3) |
| *Spirobolus marginatus* | Endogenous nocturnal | 960.0 | (4) |

From this table we see three activity indices, well spread out over the range of the scale. The chipmunk A. I. is for the first ten trials only, since the rhythm tends to shift rapidly under constant conditions of darkness, temperature and humidity. This may indicate a high degree of habitual endogenosity in this species, but the work on the animal has just begun. The cave crayfish A. I. is based on ample data, and the A. I. for the milliped is within the expected range for the species.

## SUMMARY

A discussion of the quantitative estimation of organismal activity is given, and certain mathematical suggestions are made to implement the quantitative study of rhythmicity.

## LITERATURE CITED

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